植物研究雑誌
J. Jpn. Bot.
72: 286–292 (1997)

Phylogenetic and Taxonomic Studies on *Helonias, Ypsilandra* and *Heloniopsis*

I. Comparison of Character States (2)

Noriyuki TANAKA

Department of Education, School of Liberal Arts, Teikyo University
359 Ôtsuka, Hachiôji-shi, Tokyo, 192-03 JAPAN

(Received on December 2, 1996)

Ten characters of both floral and vegetative parts were compared in the ten species of the three genera; *Helonias, Ypsilandra* and *Heloniopsis*. In each of the following pairs of character states, the former was regarded as plesiomorphic compared with the latter in this plant group; i.e., nearly flat to very slightly concave nectary – deep sheath-like saccate nectary; raceme – umbel; ebracteate inflorescence – bracteate inflorescence; relatively thick leaves – thin leaves; flowering in spring – flowering in summer to autumn; weak protandry – weak protogyny; relatively many flowers per inflorescence – few flowers. The results of observations on the floral scent, colour and nectar were also recorded. Based on all these observations, the evolutionary relationships among the species were presumed.

(Continued from J. Jpn. Bot. **72**: 221–228, 1997)

In my preceding study (Tanaka 1997c), several characters of both pistils and stamens were compared in the ten species of the three genera. In the present study, several other characters were also compared in these species, and the result is recorded here.

The species investigated here are as follows; one species of *Helonias* (*H. bullata* L.), four species of *Ypsilandra* (*Y. yunnanensis* W.W. Smith & J.F. Jeffrey, *Y. alpina* Wang & Tang, *Y. cavaleriei* Lévl. & Vaniot, *Y. thibetica* Franch.), and five species of *Heloniopsis* (*H. leucantha* (Koidz.) Honda, *H. umbellata* Baker, *H. kawanoi* (Koidz.) Honda, *H. orientalis* (Thunb.) C. Tanaka, and *H. breviscapa* Maxim.). The materials and the research methods employed in this study are the same as those described in my previous papers (Tanaka 1997a, 1997b).

Results and Discussion

As in my preceding paper (Tanaka 1997c), the name of each species is abbreviated as follows in the following description: *Helonias bullata* = ***Bu***, *Ypsilandra yunnanensis* = ***Y***, *Y. alpina* = ***A***, *Y. cavaleriei* = ***C***, *Y. thibetica* = ***T***, *Heloniopsis leucantha* = ***L***, *H. umbellata* = ***U***, *H. kawanoi* = ***K***, *H. orientalis* = ***O***, and *H. breviscapa* = ***Br***.

(1) Some floral characters

1-A. Nectar-secretion

The secretion of nectar is observed in the living plants of *Bu*, *T* and five species of *Heloniopsis* (*L*, *U*, *K*, *O* and *Br*) (Tanaka 1997a, 1997b). However, there seems to be some variation regarding the nectar-secretion in *K*. I have observed that some plants or some tepals of a flower of *K* do not secrete any nectar. In all of these species, the nectary is located at the base of the ventral side of each tepal. As for *Y*, *A* and *C*, no living material was available, so I could not confirm directly the presence of the nectar-secretion in these species. But, judging from the morphology of the basal part of the tepal, it is very likely that these species also secrete nectar (Tanaka 1997a).

1-B. **Nectaries**

In *Helonias* and *Ypsilandra*, the nectary is almost flat or slightly concave (Tanaka 1997a). In *L* and *U*, the nectary is apparently concave, being shaped like a shallow bowl or basin. The nectary of *K* is also concave, but it is very shallow. In *O* and *Br*, each tepal is adnate basally to its corresponding filament and forms a relatively deep sheath-like saccate nectary (Tanaka 1997b).

In general, the structure on the lower level of development can be regarded as more primitive as compared with that on the higher level of development. If this rule is applied to the nectary structure of this plant group, the following view can be drawn. That is, *Helonias* and *Ypsilandra* are most primitive; *L*, *U* and *K* more advanced; and *O* and *Br* most advanced, with respect to the nectary structure. A relatively shallow nectary concave and an occasional non-secretion of nectar in *K* might be derived character states.

1-C. **Colour of flowers**

The floral colour of each species is as follows: *Bu*, pink (Fig. 1A). *Y*, white (Smith and Jeffrey 1916), or pale purple (Anonymous 1976); *Y. yunnanensis* var. *himalaica*, pale blue, whitish or reddish-brown (Noltie 1994); *Y. yunnanensis* var. *micrantha*, white or yellowish white (Anonymous 1976). *A*, chocolate (Wang and Tang 1936, based on the note given by F. Kingdon-Ward on the label of his specimen, n. 7084, in K), or yellow (Chen 1980). *C*, pink or white (Chen 1980). *T*, white (Figs. 1B & 2A), pale pink, or purple (Chen 1980). *L*, white (Figs. 1C & 2C), occasionally slightly tinged pinkish. *U* (Fig. 1D) and *K*, pale pink to white. *O*, usually pink (Figs. 1E & 2E). *Br*, white or tinged pinkish (Fig. 1F).

1-D. **Scent**

In Curtis's Botanical Magazine (vol. 20, t. 747, 1804), there is a description stating that *Helonias bullata* has no scent, but I confirmed that the flowers of this species are fragrant. The fragrance is neither strong nor weak. Gleason (1952) also described the flowers of *Helonias* as having a fragrance. The flowers of *Y* are malodorous, according to the note given by G. Forrest on the label of his specimen, no. 12055, in E (this note is also cited by Smith and Jeffrey 1916), and the flowers of its variety *himalaica* are reported also to be unpleasantly scented (Noltie 1994). There has been no report regarding the scent of the flowers of both *A* and *C*. I was also unable to examine whether or not these species have a scent, because no living material was available. Both *T* and *U* have a relatively strong fragrance. The scent of *L* is very weak. *K* has also a weak scent. *O* seems to have almost no scent. *Br* has a very weak scent. Except for the malodorous scent of *Y* and its variety *himalaica* reported in the above literature, the scent I confirmed in other species was sweet.

Presumably, there are two different types of pollinators foraging on the flowers of this plant group; one is attracted by the floral scent, while the other is not necessarily attracted by the scent. The species with the flowers having a weak or almost no scent might be adapted more to the latter type of pollinators.

(2) **Dichogamy**

It is known that the flowers of *O* are protogynous (Takahashi 1988, Kawano 1989). In the present study, it was confirmed that this character is present not only in *O* but also in four other species of *Heloniopsis* (*L*, *U*, *K* and *Br*) and in one species of *Ypsilandra* (*T*) (Figs. 2A–2F). In the very young flowers of these species that are beginning to bloom, a stigma emerges from the perianth earlier than the anthers, and the surface of the stigma looks to

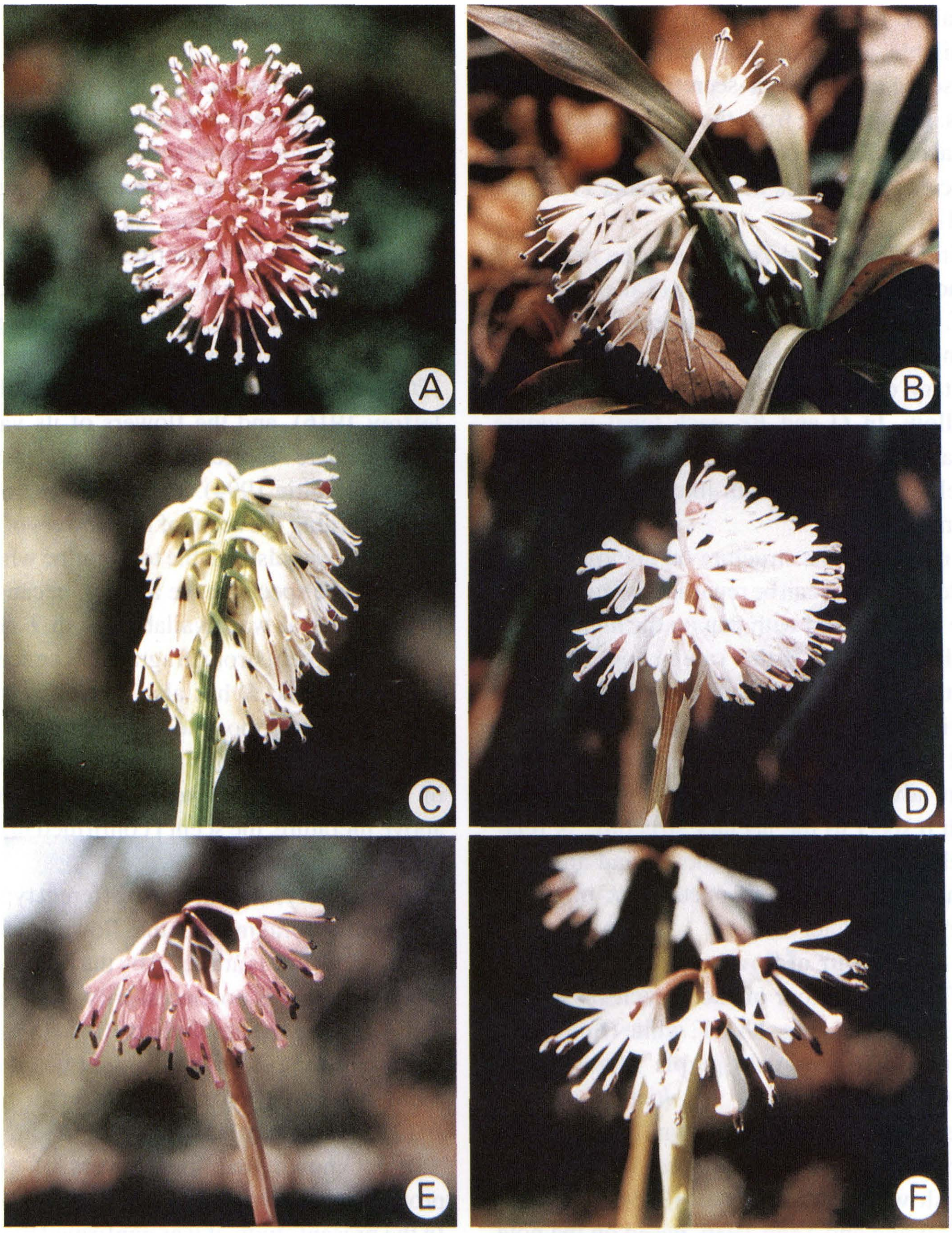

Fig. 1. Inflorescence of *Helonias*, *Ypsilandra* and *Heloniopsis*. A. *Helonias bullata* (from Edinburgh Bot. Gard., c.f. Tanaka 1997a). B. *Y. thibetica* (cult. plant, Tanaka 1997a). C. *Heloniopsis leucantha* (L-2, Tanaka 1997b). D. *Heloniopsis umbellata* (U-1, Tanaka 1997b). E. *Heloniopsis orientalis* (O-8, Tanaka 1997b). F. *Heloniopsis breviscapa* (B-4, Tanaka 1997b). In brackets is indicated the source of material. All the photographs were taken at the nurseries of Teikyo University, Tokyo. For explanations see the text.

be well receptive of pollen, while the anthers still remain undehiscent. On the contrary, in *Bu*, the flowers seem to be slightly protandrous. In these flowers (*Bu*), the anthers fairly exceed the stigmata in height, and the former appears to dehisce slightly earlier than the full development of the stigmatic surface. In all of these species mentioned above, there is a considerable overlap in the maturation period between the anthers and the stigmata. As for *Y*, *A* and *C*, no living material was available, and so I could not examine whether the flowers of these species show any dichogamy or not. There is a good possibility that a transition of the character state from weak protandry (*Bu*) to weak protogyny (*T* and *Heloniopsis*) took place during the evolutionary process of these three species (*Y*, *A* and *C*).

(3) **Inflorescence**

3-A. **Structure**

Helonias (Fig. 1A), *Ypsilandra* (Figs. 1B & 2A) and *L* (Fig. 1C) have a typical raceme. But I have observed in the cultivated condition (in Tokyo) that the upper part of the inflorescence of *L* rarely becomes compact, forming almost a subumbellate inflorescence. *U* has usually a typical umbel (Fig. 1D). *K* has usually an umbellate to subumbellate inflorescence, but occasionally a racemose inflorescence. *O* (Figs. 1E & 2E) and *Br* (Fig. 1F) have an umbellate to subumbellate inflorescence in anthesis, which often elongates after anthesis to form a racemose inflorescence.

In the three genera, the species regarded as relatively primitive in some respects [e.g., the stylar structure (Tanaka 1997c) and the nectary structure (1-B in this report)] possess a raceme, while the species regarded as relatively advanced possess an umbel. A raceme is common among the genera of Melanthioideae-Helonieae (Liliaceae), to which the three genera here concerned belong (Krause 1930), while an umbel is rare in the same tribe. An umbel itself seems to be a derived inflorescence from a raceme in origin, because the former structure is formed by aggregation of the unitary structures (pedicellate flowers). From all these observations, I regard the raceme as being plesiomorphic compared with the umbel in this plant group, and think that the species possessing the raceme (*Helonias*, *Ypsilandra* and *L*) are more primitive than those possessing the umbel (*U*, *K*, *O* and *Br*).

3-B. **Number of flowers**

The number of flowers per inflorescence was counted for each species, and the result is as follows; *Bu*, c.30–c.72. *Y*, 5–15. *A*, 2–3. *C*, 9–20. *T*, 9–46. *L*, 8–36. *U*, 2–14. *K*, 1–10. *O*, 2–11. *Br*, 1–11.

Judging from this result, *Bu* seems to bear more flowers than the other species (cf. Fig. 1).

(4) **Bracts**

The inflorescence of the three genera seems basically ebracteate (Figs. 1B–1F, and 2A). However, a few bracts occasionally appear in the inflorescence of some species like *L*, *U* and *O*. On the contrary, the inflorescence of *K* is usually bracteate.

(5) **Leaves**

The leaves of *Br* are slightly thinner in texture [Ohwi 1953 (under the name of *Heloniopsis orientalis* var. *flavida*), 1965, 1975, Kitamura et al. 1964 (under the name of *Heloniopsis orientalis* var. *flavida*), my own observation] compared with those in most of the other species (the leaves of *K* also look to be slightly thinner than those in the other species except *Br*, but this point needs to be examined more elaborately in the future).

(6) **Flowering season**

Generally speaking, the flowering season of the three genera, except one species (*K*), is spring (Feb.–May), but the season naturally fluctuates to some extent according to the geographical and/or ecological condition of the habitats; i.e., plants in alpine regions and/or in northern districts tend to flower late (even in Jul. to early Aug.), while those in warm

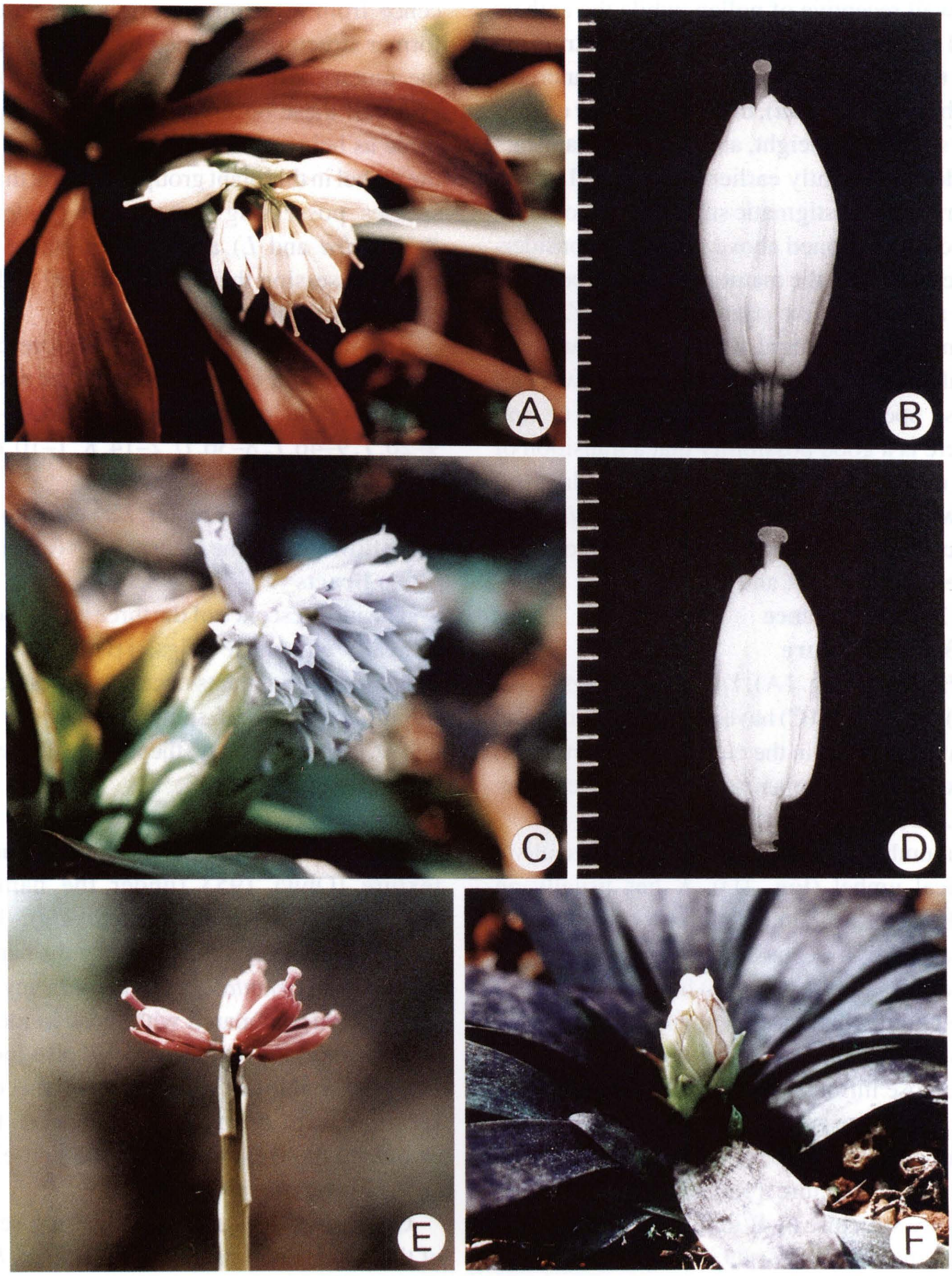

Fig. 2. Protogyny in *Ypsilandra* and *Heloniopsis*. A, B. *Y. thibetica* (cult. plant, c.f. Tanaka 1997a). C. *H. leucantha* (L-1, Tanaka 1997b). D. *H. umbellata* (U-1, Tanaka 1997b). E. *H. orientalis* (O-8, Tanaka 1997b). F. *H. breviscapa* (B-3, Tanaka 1997b). In brackets is indicated the source of material. All the photographs except B and D were taken at the nurseries of Teikyo University, Tokyo. Scale in Figs. B and D in mm.

districts tend to flower early (even in Jan.). Contrarily, *K* flowers in (late) summer to autumn (Aug.–Oct.).

In my preceding paper (Tanaka 1997c), I suggested that the evolution of the species of the three genera has proceeded in the following order; $Bu \rightarrow Y \rightarrow A \rightarrow [C, T]^* \rightarrow [L, U, K]^* \rightarrow O \rightarrow Br$ (*the relationships between the species within the brackets remain to be studied). According to this scheme, the evolution has proceeded from *Helonias* through *Ypsilandra* to *Heloniopsis*. There seems to be no particular discrepancy between this scheme and the results obtained in the present study. For example, the observations on both the nectary (cf. 1-B of this paper) and the inflorescence (cf. 3-A) do not contradict the above scheme. The results obtained in the present study further provide some clues to clarify the evolutionary process of this plant group. That is, the comparison of the inflorescence (cf. 3-A) suggests that *L* is more primitive than *U* and *K* with respect to this structure. The comparison of various character states (e.g., 1-B, 3-A, etc.) suggests that *U* is the closest relative of *K*. The results also show that *K* is a species having some unique character states like 'flowering in summer to autumn' (cf. 6) and 'bracteate inflorescence' (cf. 4), both of which can be regarded as derived characters. The overall small plant size in *K* (Hatusima 1975, Walker 1976, my own observation) seems also to be an apomorphic attribute. The relatively thin texture of the leaves of *Br* (cf. 5) might also be an apomorphy. From all these observations, it is presumed that the evolution of the species of the three genera has proceeded in the following order:

$$\begin{tikzcd} & & & & & & K & \\ Bu \arrow[r] & Y \arrow[r] & A \arrow[r] & {[C \bullet T]^*} \arrow[r] & L \arrow[r] & U \arrow[r] \arrow[ur] & O \arrow[r] & Br \end{tikzcd}$$

(*the relationship between *C* and *T* needs further study)

If this scheme is correct, each of the following characters is likely to have evolved as follows; i.e., the flowers were at first slightly protandrous, but later became protogynous (cf. 2). The floral colour was originally pink, but later fluctuated to some extent (cf. 1-C). The flowers had initially a sweet fragrance, but later underwent some fluctuation (cf. 1-D). The number of flowers per inflorescence was initially relatively many, but later decreased to some extent (cf. 3-B). Ebracteate inflorescence (cf. 4), relatively thick texture of leaves (cf. 5), and flowering in spring (cf. 6) are all considered to be plesiomorphic in state, compared respectively to bracteate inflorescence, thin leaves, and flowering in summer to autumn, in this plant group.

Further synthetic discussion on the evolutionary facets of this plant group will be made in my forthcoming paper.

References

Anonymous 1976. *Ypsilandra.* Iconographia Cormophytorum Sinicorum. Tomus **5**, p. 425. Science Press, Beijing (in Chinese).

Chen S-c. 1980. *Ypsilandra. In*: Wang F.-t. and Tang T. (ed.), Flora Reipublicae Popularis Sinicae, Tomus **14**, pp. 15–18. Science Press, Beijing (in Chinese).

Gleason H. A. 1952. *Helonias.* The New Britton and Brown Illustrated Flora of the Northern United States and Adjacent Canada, p. 406. Hafner Press, New York.

Hatusima S. 1975. *Heloniopsis.* Flora of the Ryukyus (Added and Corrected), pp. 786–787. Okinawa Seibutsu-kyôiku Kenkyûkai, Naha (in Japanese).

Kawano S. 1989. Difference in habitats and life history, *In*: Kawano, S., compil. Life history of *Heloniopsis*, pp. 88–115 [pp. 108–111]. Newton Special Issue. Shokubutsu no Sekai, no. 4. Kyoikusha, Tokyo (in Japanese)

Kitamura S., Murata G. and Koyama T. 1964. *Heloniopsis.* Coloured Illustrations of Herbaceons Plants of Japan III (Monocoty ledoneae), pp. 151–152. Hoikusha, Osaka (in Japanese).

Krause K. 1930. Melanthioideae-Helonieae. *In*: Engler A. und Prantl K. (ed.), Die Natürlichen Pflanzenfamilien. **15a**: 257–260. Verlag v. Wilhelm Engelmann, Leipzig.

Noltie H. J. 1994. *Ypsilandra.* Flora of Bhutan. Vol. **3**(1), p. 90. Royal Botanic Garden Edinburgh, Edinburgh.

Ohwi J. 1953. *Heloniopsis.* Flora of Japan 1st ed., pp. 285–286. Shibundo, Tokyo.

——— 1965. *Heloniopsis.* Flora of Japan (in English), p. 284. Smithsonian Institution, Washington, D.C.

——— 1975. *Heloniopsis.* Flora of Japan, new ed. revised and

enlarged, p. 336. Shibundo, Tokyo.

Smith W. W. and Jeffrey J. F. 1916. *Ypsilandra yunnanensis*. Notes Roy. Bot. Gard. Edinb. **9**: 143–144.

Takahashi H. 1988. The pollination biology of *Heloniopsis orientalis* (Thunb.) C. Tanaka (Liliaceae). Pl. Sp. Biol. **3**: 117–123.

Tanaka N. 1997a. Taxonomic significance of some floral characters in *Helonias* and *Ypsilandra* (Liliaceae). J. Jpn. Bot. **72**: 110–116.

——— 1997b. Evolutionary significance of the variation of the floral structure of *Heloniopsis*. J. Jpn. Bot. **72**: 131–138.

——— 1997c. Phylogenetic and taxonomic studies on *Helonias*, *Ypsilandra* and *Heloniopsis*. I. Comparison of character states (1). J. Jpn. Bot. **72**: 221–228.

Walker E. H. 1976. *Heloniopsis*. Flora of Okinawa and the Southern Ryukyu Islands, pp. 304–305. Smithsonian Institution Press, Washington, D.C.

Wang F. T. and Tang T. 1936. *Ypsilandra alpina*, p. 81. Notes on Chinese Liliaceae III. Bull. Fan Mem. Inst. Biol. Bot. **7**: 81–90.

田中教之：***Helonias*, *Ypsilandra*, *Heloniopsis***の系統と分類 **I.** 形質状態の比較 **(2)**

3属10種の10形質について比較研究を行った．これらの種群に限って言えば，次の各形質の前にあげる形質状態はplesiomorphicであり，後にあげる形質状態はapomorphicであると筆者は考える：総状花序－散形花序，無苞の花序－有苞の花序，比較的厚手の葉－薄手の葉，春季の開花－夏～秋季の開花，花被片基部の平坦ないし極めて浅い蜜槽－花被片とそれに対生する花糸が基部で合生して形成するやや深い鞘状の蜜槽，比較的多い花数－少ない花数．また，これらの種群の花色，蜜の分泌，花の香，雌雄ずいの熟期についても記録した．*Helonias*ではごくわずかながら雄ずい先熟の傾向があるように思われる．これに対して，*Ypsilandra thibetica*と*Heloniopsis*（ショウジョウバカマ属）の5種では雌ずい先熟の傾向がある．これらのすべての観察事実を踏まえて，種間関係を進化的観点から検討した．3属の系統進化，地理的分布，および分類等についての問題は今後の報文の中でさらに詳しく検討していく予定である．

(帝京大学文学部教育学科)